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Notes on the Haustoria of some N. A. Parasitic Phanerogams.*

By JOSEPH SCHRENK.

(Plate XLVI.)

GERARDIA QUERCIFOLIA, Pursh.—The parasitism of *Gerardia* seems to have been first pointed out by J. Stauffer, who, in a curious little pamphlet of two pages, printed by the author in 1850, mentions the parasitic attachments of *Gerardia flava*, *quercifolia*, *pedicularia* and *tenuifolia*.† On two accompanying plates portions of specimens of these four species are figured. The character of these illustrations may be judged of by a reproduction of one of them in Gray's Structural Botany, p. 38. Neither text nor figures contain any information about the interior structure of the haustoria, nor was I able to discover any literature referring to this subject anywhere else.

The figures on Plate xlv. (with one exception) were drawn from the haustoria of *Gerardia quercifolia* attached to the roots of *Corylus rostrata*, Ait., gathered in New Hampshire, in the month of August, and on them the following description is mainly based. Besides, I examined the haustoria of *Gerardia flava*, L., *pedicularia*, L., *tenuifolia*, Vahl., *purpurea*, L., and *maritima*, Raf. The two latter species, to my knowledge, have not yet been reported as parasitic.

The haustoria of *Gerardia* appear as lateral rounded excrescences which are scattered irregularly along the branches of the root, wherever there is a chance for them to obtain suitable nourishment: they very frequently attach themselves to the root of the *Gerardia* itself. The largest I found are about 6^{mm}. in length, while the smallest consist simply of a few layers of cells raised above the surface of the root. We either find several, often many, haustoria, more or less distant from one another, growing from the same branch of the *Gerardia* root, which keeps on growing, eventually producing more haustoria (Fig. 7; at *cm* we see the continuation of the root); or the rootlet, after having produced a haustorium, shrinks into an insignificant appendage (Fig. 1), or disappears altogether, so that the haustorium appears terminal (Figs. 2, 3, 4).

* Cf. BULLETIN, Vol. x., No. 4.

† When I sent the note referring to the parasitism of *Gerardia tenuifolia* to the BULLETIN, in December 1883, I had not yet seen this pamphlet; a copy of it was found in the library of the Torrey Herbarium by Dr. N. L. Britton, who drew my attention to it, and thereby enables me to give the credit of having discovered the parasitism of *G. tenuifolia* to Mr. Stauffer. In this pamphlet *Comandra umbellata* also is briefly described, and two accompanying plates, lithographed and printed by the author, give a good representation of the entire plant above ground, and a fair one of its roots.

At the earliest stages of their development which I examined, the haustoria form slight excrescences from the cortical portion of the *Gerardia* root, in such a way that the epidermis forms an unbroken covering of both root and haustorium. On young haustoria I noticed some papillose superficial cells which looked exactly like short root-hairs, but their principal function evidently is to take hold of some contiguous foster-root. The youngest haustoria do not contain any vascular tissue, but soon there appear in the axial portion single threads of reticulated vessels connecting the apex of the haustorium with the fibro-vascular tissue of its mother-root. At the same time the haustorium increases in all its parts and finally appears as figured on the plate.

As I called the haustorium an outgrowth of the root, and as the tissues of the latter are continuous with those of the former, I will, in the first place, give a brief description of the root of our *Gerardia*.

In the centre of the root there is a fibro-vascular cylinder; its diameter is usually equal to about one-half the diameter of the entire root. This cylinder contains very wide reticulated vessels and thick-walled wood-cells; it is surrounded by a narrow zone of cambium beyond which we find large parenchymatous cells with many inter-cellular spaces. Irregularly scattered in the parenchyma we see numerous sclerenchyma cells, singly or in groups from 2 to 6, mostly of prismatic shape; their walls are exceedingly thick and pierced by branching canals. The zone of parenchyma around the central wood cylinder is divided about midway by a layer of closely arranged cells. This layer seems to be a true endodermis; its cells are very narrow compared to the surrounding parenchyma cells; the partitions separating them are strictly radial and frequently undulating, and the cell-walls resist the action of sulphuric and even of chromic acid. Inside of this ring the starch granules in the parenchyma cells are much smaller than in those outside of it, where they are quite large.

At the circumference of the root there is a single layer of epidermoidal* cells the outside walls of which are thickened and even more resistant against the action of the reagents mentioned above than are the walls of the endodermis. The surface view of the root shows that these cells are arranged in oval, frequently elongated hexagonal plates or patches. The middle portion of such a group is formed of rows of two or three cells each; the cells are separated by radial (and vertical) partitions which are still more wavy than those found in the endodermis.

At first I was inclined to consider this epidermoidal layer as the true epidermis, and to explain the absence of root-hairs by the parasitic nature of the plant; but, on closer examination, I soon found that the supposed epidermis was covered with a continuous layer of very long, exceedingly thin-walled, empty cells, which, on the cross-section, show quite an irregular outline (Figs. 5 and 7, *e*). Owing to the tenderness of their membranes it is not easy to obtain transverse sections that will show these cells completely encircling the root, and

* This term is used by v. Höhnelt, Olivier and others to designate a layer of cells close to the epidermis, that resembles in most respects the endodermis.

it is still more difficult to prepare perfect longitudinal sections. However, I never failed to see this epidermis, as I must call it, on thin, *i. e.* young portions of the *Gerardia* root, while on older ones I could, at best, make out a few shreds only. I must therefore suppose that the epidermis is soon cast off. I am not prepared to assert that these epidermal cells perform the functions pertaining to root-hairs, but, considering the thinness of their membranes, which do not seem to be cuticularized, and their peculiar inflated form, I do not see what should prevent them from absorbing the water from the soil in case the plant needed it.

Referring to this description of the root, the structure of the haustorium itself will be more easily understood. With *Gerardia*, the body of the root from which the haustorium grows, contributes a much greater share to the bulk of the haustorium than with *Comandra*. We can see from Figs. 5 and 7 that a considerable portion of the upper half of the haustorium really belongs to the root proper. In Fig. 5, representing a longitudinal section of a hazel-root that bears a haustorium in the manner illustrated by Fig. 3, the vascular cells of the *Gerardia* root, *pl*, appear cut across, for it had grown at right angles with the foster-root. In Fig. 7 the vessels of the *Gerardia* root, *pl*, are viewed longitudinally, *Gerardia* and hazel-roots lying in the same plane.

The epidermoidal layer of the haustorium is continuous with that of its root (Figs 5 and 7, *ep*), and the epidermis, *e*, is also met with on the haustorium. It is found especially well preserved in the angles at which the haustorium and the foster-root meet (Figs. 5 and 7, *e*). In and near these places the epidermis-cells have so multiplied as to form several irregular layers; no doubt, they help the *Gerardia* to get a better hold of its host.

The portion of the haustorium-bark underneath the epidermis, *bk*, is likewise a continuation of the root-bark. The parenchyma cells near the epidermis are larger than those nearer the centre; the former contain much larger starch-grains. The endodermis of the root is also continued in the upper part of the haustorium; in Fig. 6, it is indicated by a dotted line, *en*. The sclerenchyma-cells are of the same structure and similarly arranged in both root and haustorium; they are, as a rule, more numerous in old haustoria. The cortical portion does not penetrate into the foster-root, but ends at its surface.

From the central wood-cylinder of the root very numerous vessels, surrounded by a zone of cambium, spread downward like an umbrella, but in a solid mass, Figs. 5 and 7, *vs*. Before they reach the middle of the haustorium most of them end abruptly, anastomosing, however, by means of short connecting vessels. Many of these vessels continue their course, singly, through the lower part of the haustorium to its apex, until they reach the wood tissue of the foster-root (Figs. 5, 6, 7 and 8). They consist of comparatively short links, the ends of which are laterally connected, and are transformed into continuous passages in the usual manner, by the absorption of their septa.

These vascular fibres are accompanied, in their lower course, with elongated, active cells, *ac*, which constitute the meristematic tissue

within which the growth of the apex takes place. In the central part of every haustorium, just below the solid mass of descending vessels, there is a layer of considerable thickness which, except at its centre, is formed of regular rows of oblong cells that are flattened contrary to the vertical axis of the haustorium. The centre of this layer consists of rounded, irregularly arranged cells (Figs. 5 and 7). All the cells of this central portion contain a turbid, granular protoplasm, so that after staining with carmine they become quite conspicuous.

The contact of the tissues of the parasite with those of the foster-root is similar to that which we observed in *Comandra*. I satisfied myself that there is a perfectly open communication between them. The meristematic, active cells enter the vessels of the foster-root bodily after the walls of the latter have been partly absorbed, Figs. 10 and 11. Some vessels are formed in the haustorium, at the side of a vessel of the foster-root, and then the side-wall of the latter and the end walls of the former are absorbed, Fig. 13; or they meet end to end, and then they simply form one passage after the absorption of the end-walls, Fig. 9.

But more interesting and more important than all these facts I consider the following observation that I wish to record on this occasion.

In ever so many haustoria of *G. quercifolia* and, in a still more exquisite manner, of *G. flava*, I found almost all their vascular cells connected with those of the foster-root in such a way, that communication was open between the parasite and the stem of the foster-plant, while communication between parasite and peripheral ends of the foster-root was entirely cut off. In Fig. 5 the right-hand side of the foster-root, at *w*, if not cut off, would lead to the main root, and that to the stem. We observe that the tissues at the left, toward the root end were absorbed and replaced by the apex of the haustorium and that none of the entering vascular fibres turns that way. In Fig. 7 the left hand side points towards the stem. The process begun in these two cases has been completed in the one illustrated by Fig. 8. The apex of the haustorium gradually worked its way deeper and deeper into the hazel-root, while its tissues kept turning steadily in one direction: toward the stem, away from the root-end, until finally the latter was cut off completely and the haustorium took its place. The progress of this process may be seen in its various stages by examining some typical forms of the *Gerardia* haustorium, as illustrated by Figs. 1, 3, 2 and 4.

I have some slides with sections taken from *G. flava* which show the tendency of the apex to turn away from the root-ends in a remarkably clear manner. That portion of the apex which would correspond to the portion lying to the right of the point *x*, in Fig. 7, or to the left of *x* in Fig. 5 (*i. e.* toward the root-end), is *separated* from the tissues of the foster-plant, for the outermost cells of this part of the haustorium have their *outer* walls lignified, as shown by the indol and other reactions. At the same time, the adjacent cells of the foster-root are found to be in a state of partial decomposition, while on the opposite side the connection between parasite and host is perfect, as shown by Figs. 10 and 11 which were drawn from one of these slides.

I said above that haustoria are very frequently found attached to the roots of *Gerardia* itself. Such haustoria have either the shape of those already described (Figs. 1-4), or they are mere cylindrical branches growing at right angles *from* some *Gerardia* rootlet *into* another contiguous one. But, instead of single threads of vascular cells as described above, all these haustoria have solid, massive cylinders of vessels connecting the root *from* which, with the root *on* which they grow. In these haustoria I could not detect the remarkable tendency of the apical tissues to meet the descending sap-current of the foster-plant, the vessels are generally inserted at right angles with the wood cylinder of the *Gerardia* root.

In some *Gerardia* rootlets infested with haustoria I found the vessels in the immediate vicinity of the haustorium apex filled with those hernioid protrusions which were observed by some histologists* growing in vessels surrounded by very active cells. The walls of these active cells will bulge out through the pits of a vessel into its cavity; then they will grow considerably, forming globular cells, and will eventually close up the vessel entirely. In the sections that I have examined the walls of these hernioid cells seem to be lignified; at least, they appear of the same color as the vessels enclosing them after staining the sections with alum carmine and aniline green.

If I had found these "puzzling"† hernioid protrusions near all, or at least near very many of the haustoria examined, I should not hesitate to consider them as a contrivance to defend the *Gerardia* against the senseless depredations of its own haustoria.

I abstain, for the present, from drawing the conclusions in reference to the nature of parasitism in general, which are most forcibly suggested by the above premises.‡ Besides, if these observations should prove correct, they might contribute, to a certain extent, to the solution of another much discussed, and still undecided,§ physiological question—the question about the functions which the tracheary tissues perform in the transmission of the various fluids necessary to the life of plants.

We have seen that in the parasites examined thus far the *channels* or cavities of the vessels are in close, open connection with the cell-cavities of the foster-root. Shall we still assume that it is only *air* which passes within these united channels? And must we still suppose that the water in plants travels within the *substance* of the walls of these vessels, and not within their cavities?

Hoboken, August, 1884.

* De Bary, *Vergleichende Anatomie*, p. 594 ("Thyllen"); J. C. Arthur in Ch. E. Bessey, Botany, p. 30.

† Bessey, l. c.

‡ *E. g.* it is very doubtful whether the following assertion, found in Sachs (Lehrbuch, 4th ed., p. 690, foot-note) will hold good: "Parasites containing much chlorophyll, like the Loranthaceæ, are able themselves to assimilate, consequently they need to take only water and mineral substances from their foster-plants."

§ Haberlandt, *Physiologische Pflanzenanatomie* (1884), p. 209: "The physiological nature of the vessels and tracheids has been discussed very frequently; still this question has not yet been definitively solved."

EXPLANATION OF PLATE XLVI.—Figs. 1, 2, 3, 4. Haustoria on hazel-root about $\times 8$, (see text). Fig. 5. Longitudinal section of haustorium and hazel-root of the same form and arrangement as those of Fig. 3. *e*, epidermis; *ep*, epidermoidal layer; *bk*, bark (parenchyma and sclerenchyma cells); *cm*, cambium; *pl*, central wood cylinder of *Gerardia*-root cut across; *ac*, meristematic tissue; *b*, epidermis and bark of hazel-root; *c*, cambium; *w*, wood tissue; *G*, portion of the haustorial apex that has worked its way around the wood-cylinder of the foster-root to its lower side (*cf.* Fig. 3); *D*, large pitted duct of *Corylus* with entering vessels of *Gerardia*; $\times 45$.—Fig. 6. Cross-section of both *Corylus* and *Gerardia*-roots. As the tissues of the haustorium appear in the same way as in Fig. 5, the outlines only are given. *en*, endodermis; *c*, *b*, *w*, same as in Fig. 5, $\times 25$.—Fig. 7. Longitudinal section of both *Corylus* and *Gerardia*-roots. Letters as in Fig. 5, $\times 45$.—Fig. 8. Section of a haustorium occupying the end of a rootlet, as illustrated in Fig. 2, $\times 45$.—Fig. 9. The duct *D*, Fig. 5, magnified $\times 460$. 1, large vessel of *Gerardia* cut across, showing perforated septum; 2, 3, 4, 5, smaller vessels communicating with 1 and opening into the large *Corylus*-duct; the vessel 4 shows remnants of its absorbed end wall and (below the rim) of a septum, also the scalariform thickening of its farther wall.—Figs. 10 and 11. Wood-cells of an unknown root attacked and entered by some haustorium cells of *Gerardia flava*, $\times 500$.—Fig. 12. Tangential section of hazel-root with medullary ray cut across, and with large duct *d*; *v*, cells of haustorium, $\times 135$.—Fig. 13. Duct *d*, of Fig. 12, magnified $\times 460$, to show the vessels of *Gerardia*, *v*, opening into the duct, and the cells 1 and 2 disintegrating its end wall.

All the powers given above refer to the original drawings, which, in the plate, appear reduced to one-half their size.

Kansas Fungi.*

By J. B. ELLIS and W. A. KELLERMAN.

ÆCIDIDIUM ÆSCULI.—Hypophyllous, on pale yellowish, slightly thickened spots, 4–6^{mm} in diameter. *Æcidia* orange-yellow, 30–75 on each spot, generally with a vacant space in the centre, hemispheric and closed at first, about 200 μ in diameter, at length opening above and becoming short cylindric, with an irregularly lacerated margin; spores orange-colored, irregularly globose (19–25 μ) with coarse granular contents; the component cells of the *æcidia* subhexagonal or oblong, and faintly striate, the striæ extending more or less perfectly entirely across.

On leaves of *Æsculus glabra*. May. No. 526.

ÆCIDIDIUM VERBENICOLA.—*Æcidia* hypophyllous, clustered, 3–35 together, 200–250 μ in diameter, orange-red within, covered outside with a granular, semitransparent coat like grains of sugar; margin of *æcidia* white, recurved and sublacerate-dentate; component cells subhexagonal (19–25 μ), or elongated (30–35 \times 20–25 μ), surface marked with flexuous ridges and tubercles; spores globose, elongated or subangular by compression, 19–25 μ , orange. The corresponding spots on the upper surface of the leaves are at first pale yellow but become purplish black.

On leaves of *Verbena urticifolia* (No. 532) and *V. stricta* (No. 549.) June. Possibly not distinct from *Æc. Verbena*, Speg., but differs with constantly clustered *æcidia* with recurved margin, and in not being hemispheric at first.

ÆCIDIDIUM CEANOETHI.—*Æcidia* hemispheric, closed at first, but

* The species here described were collected by Dr. W. A. Kellerman in the vicinity of Manhattan, Kansas, from May to September, 1884.

